WINTERBUD PRODUCTION AND FUNCTION IN BRASENIA SCHREBERI

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Propagule-like reproductive structures are regularly found among many of the higher aquatic Angiosperms. When such structures are dormant overwinter and germinate in the spring to produce new plants, they are generally called winterbuds. (fig. 1.) In cases where the complete life cycles of these plants have been observed, it can be reasonably said that asexual vegetative reproduction through winterbud production and dissemination plays a significant role in the seasonal maintenance and distribution of these higher aquatic plants (Arber 1963, Sculthorpe 1967). One such plant receiving only limited attention in the literature is *Brasenia Schreberi* Gmel., which produces large highly developed winterbuds (Arber 1963, Chrysler 1938) or turions (hibernacula) (Sculthorpe 1967). (fig. 3-a.)

The genus *Brasenia* is a monotypic aquatic group in the family Nymphaeaceae belonging in the subfamily Cabomboideae, the closest living relative is the genus *Cabomba*. *Brasenia* is distributed throughout the world in the temperate zones and the higher elevations of the subtropics with the exception of continental Europe. However, fossil evidence indicates that *Brasenia* grew widely throughout Europe during the Pleistocene period (Arber 1963, Engler and Prantl 1891, Fassett 1957, Ridley 1930).

No comprehensive study of the life history or ecological treatment of the genus *Brasenia* exists. Early anatomical data are available however (Schrenk 1888). In addition, Chrysler in 1938 published a limited account of the function of winterbuds of *Brasenia* based upon field observations in

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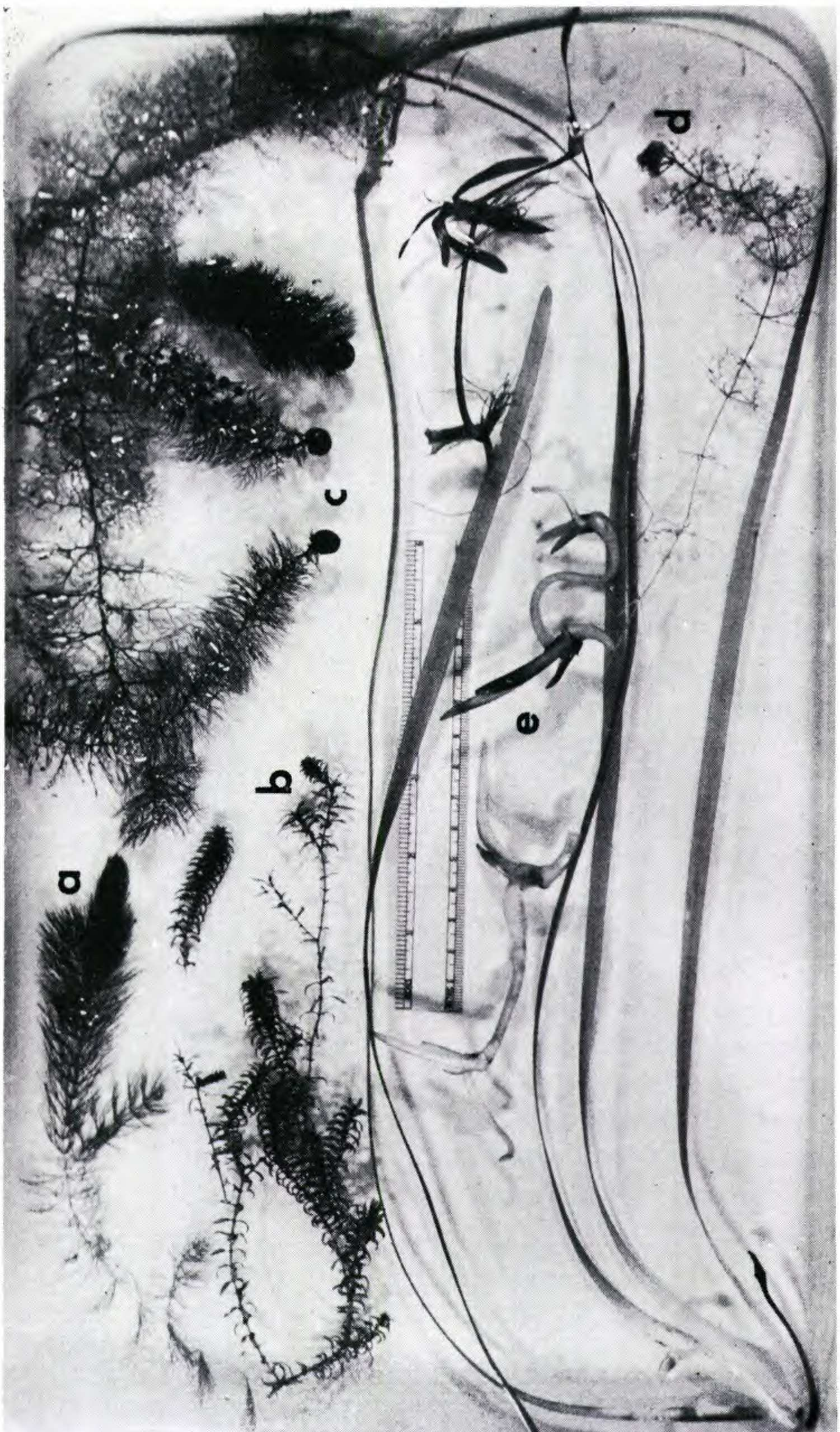
[1]This study was conducted while the author was an NDEA Graduate Fellow at the University of New Hampshire. I should like to express my gratitude to Mr. Wendell Berry, who, as a graduate student at U.N.H., assisted immeasurably in the early stages of this study. Special thanks are also due to Professors Albion R. Hodgdon and Radcliffe B. Pike for their generous assistance and encouragement throughout.


a
b
c
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e

southern Maine and laboratory experiments conducted in New Jersey with the material from Maine. Briefly, Chrysler suggests that *Brasenia* winterbuds abscise in the fall and by remaining dormant on the bottom of the pond overwinter and germinate in the spring thereby fulfilling an important reproductive function.

In a review of the aquatic Angiosperms Arber in 1963, based at least in part upon the work of Chrysler (1938), states that winterbuds of *Brasenia* are specialized structures of reproduction. In addition, Yeo in 1966, in a utilitarian study of yields of winterbuds found in the commercial water of the western Rockies and California, has reached essentially the same conclusions based upon yield data and literature references. Most recently, Sculthorpe (1967), also citing Chrysler, has provided a most convincing description of *Brasenia* winterbud (turion) production and function.

Conversely, preliminary observations conducted by the author during the 1965 season in east-central New Hampshire suggested that *Brasenia* winterbuds are not effective reproduction structures, at least at this latitude and longitude. Thus it is this question of functional vegetative propagation via winterbud production and dissemination casually observed and reported by Chrysler that the present paper attempts to resolve.

With the foregoing objective clearly defined, the task of designing an adequate research program was simplified. In order to satisfactorily understand the function of *Brasenia* winterbuds, all events that constitute the so-called "normal" life cycle of the plant would have to be routinely observed and recorded.

Two observational sites were selected on the bases of accessibility and differing ecological characteristics. One,

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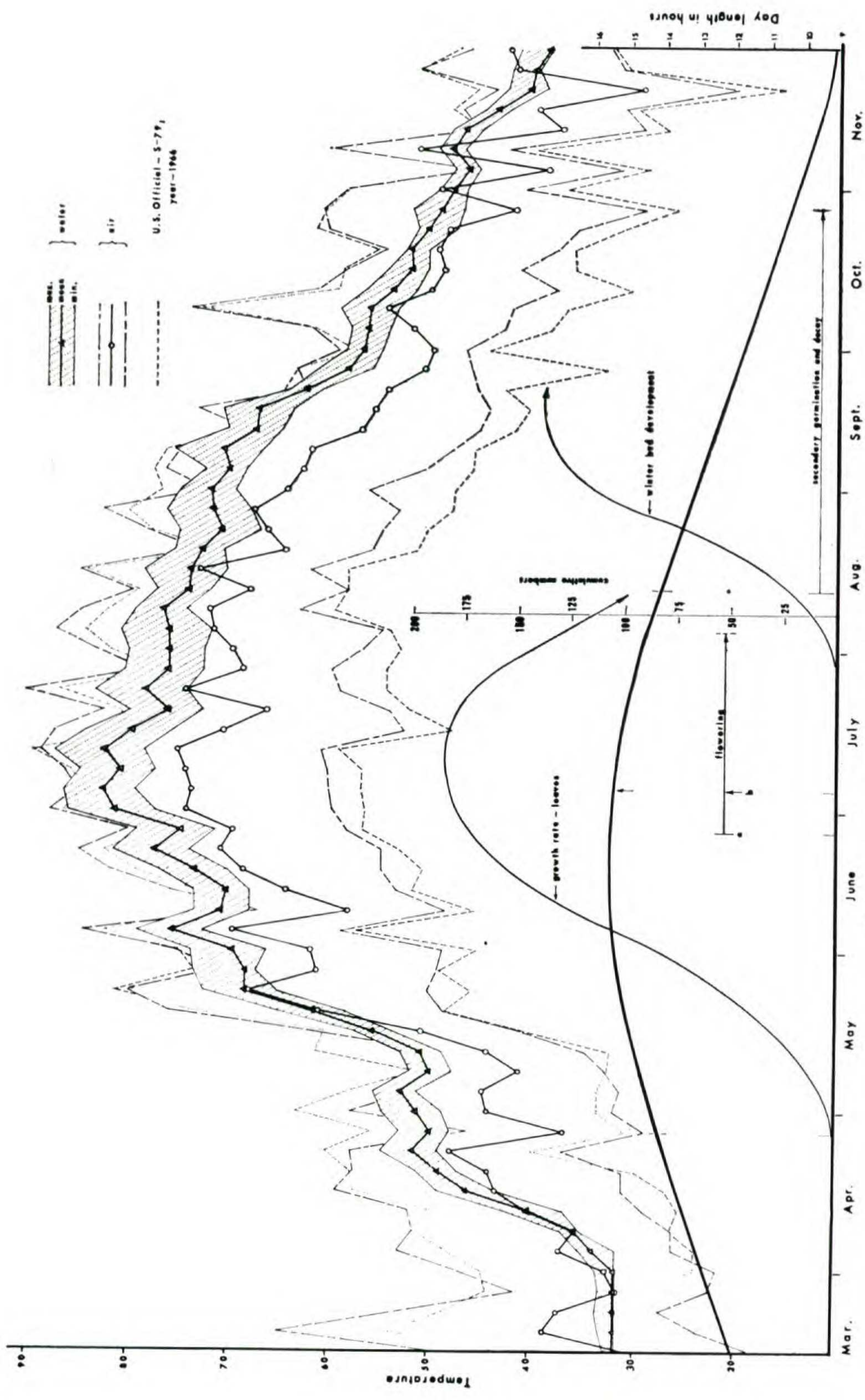
Plate 1424

Figure 1. Functional winterbuds of several aquatic vascular plants. a. *Ceratophyllum demersum* L. b. *Elodea Nuttallii* (Planch) St. John. c. *Utricularia vulgaris* L. d. *Utricularia* pupurea Walt. e. *Vallisneria americana* Michx.



BRASENIA GROWTH IN RELATION TO ENVIRONMENTAL FACTORS

Wheelwright Pond in Lee, New Hampshire: of moderate size, 100+ acres; of varying depth, one to thirty feet; of pH 6.8 to 7.4 depending upon the time of year, was selected as the primary site. Four observation stations were established which provided the bulk of the quantitative data reported herein.

The second site in Nottingham, New Hampshire on the first branch of the Little River is a small beaver dam and pond: of approximately four acres in size; of relatively uniform depth, two to eight feet; surrounded by a sphagnum swamp at the margins; of relatively acid composition, approaching pH 5.0 at times of low water, was used primarily as a confirmation station. In addition, it was possible to follow the course of winterbud distribution for several miles downstream and, most importantly, to record their fate.

Typical life history growth phenomena were observed and recorded with time throughout the 1966 growing season which included: initiation of growth; growth rates; flowering; winterbud initiation and productivity; winterbud distribution and postseasonal development including ultimate fate. Equated to temperature and photoperiod, the combined data for Wheelwright Pond are summarized in figure 2 and explained below.

A total of 10 *Brasenia* plants, selected at random within site #1, were individually identified with a tagged stake thrust securely into the bottom muck adjacent to each plant. The individual plants possessed from one to three attached winterbuds consisting of from one to three segments. (see fig. 3 and 4) Daily observations were made during the period April 11 to April 30. Initiation of growth as "germination" was recorded as having occurred when the first

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Figure 2. Summary graphical representation in time of various growth phenomena associated with the life cycle of *Brasenia Schreberi* Gmel. at Wheelwright Pond, Lee, New Hampshire, during the 1966 growing season. The phenomena of growth have been equated with temperature and photoperiod (day length) at this latitude, 43° 08′ North and Longitude, 71° 00′ West. Detailed explanation in text.

observable meristem of a winterbud was measured to have elongated one inch. Of the ten plants observed, only one failed to grow, the remaining nine plants germinated within a two day period, April 24 and 25. The process of germination was confirmed at the three remaining Wheelwright stations and Nottingham during the same period.

The initial attempt to determine growth rate as a function of meristem elongation had to be abandoned in the second week. The profusion of leaves being produced throughout the colony made it virtually impossible to relocate tagged structures from one day to the next. The remaining data were obtained as the average daily number of new leaves arriving at the surface within two sample plots, each measuring 40 × 50 feet. At best, the composite curve "growth rate-leaves" can only be presented as an approximation of real growth rates. Despite these inadequacies, the observed data are in general agreement with the literature values for hydrophytes. (Arber 1963, Sculthorpe 1967)

No attempt was made to quantitate flowering. Flowerbud initiation (a), day of flowering (b), and period of flowering are presented as they relate in time to all other observed growth phenomena. (See fig. 2.)

Since all observed active shoot apicies possess a winterbud-like morphology (containing only one segment) at all times during the growing season, it was difficult to determine precisely when initiation of true winterbuds had occurred. When a total of ten such structures were observed to have developed multiple segments, winterbud initiation was assumed to have occurred. Subsequent observations confirmed these decisions.

The curve "winterbud development" corresponds to the total number of winterbuds produced by twenty plants selected at random and observed weekly during the period July 23 to September 28.

In excess of 6,000 winterbuds were counted, examined and collected during the 1966 and 1967 seasons. In the interest of clarity, these data are presented twice. First, as the events occurred in time (see fig. 2, secondary germination and decay); second, as the events occurred quantitatively (see fig. 5, summary of winterbud activity). The significance of these data is presented in the results and discussion section below.

A "Friez" (Bendix Aviation Corporation) model 201-W dual-recording thermograph provided an accurate accounting of water and air temperatures on a continuous basis at site #1, station #1, Wheelwright Pond. The instrument was housed on a roofed but open-sided platform supported by a fixed tripod and elevated three feet above the surface of the water, twenty-five feet from shore. The air temperature probe was shaded from sun and rain but otherwise exposed to the atmosphere at all times. The remote water temperature probe was located on the shaded side of the north oriented leg of the tripod at a depth of 55 cm., the average depth of attached winterbuds observed at the site at the time of installation.

The temperature data were averaged, means calculated (mean low, mean, mean high), and plotted on the basis of four day intervals for each parameter, water and air. Official U. S. Weather Bureau Station S-79, Durham, New Hampshire, data were averaged and the four day means plotted to indicate the range of differences between atmospheric temperatures over land and water. For convenience, all temperatures are expressed in Fahrenheit.

Photoperiodicity, expressed as "day length in hours," was calculated from official U. S. Coast and Geodetic Survey Sunrise and Sunset Tables (U. S. Department of Commerce 1966) for Boston, Massachusetts, and corrected to Latitude 43° 08′ North and Longitude 71° 00′ West, the geographical location of Wheelwright Pond.

An experiment designed to test the winterbud's ability to germinate in relation to water depth was conducted at the Wheelwright Pond Site #1. A long upright stake was driven securely into the bottom muck in nine feet of water. At two foot intervals from the surface downward were attached four 6″ × 8″ perforated cans with clear polyethylene covers containing three winterbuds each; the cans were arranged vertically along the south-facing side of the stake. The entire apparatus was installed in place on December 2, 1965 and retained throughout the winter and spring seasons. Surface observations were made weekly throughout and the winterbuds collected on June 11, 1966. (See fig. 4.)

An experiment designed to test the effectiveness of the winterbud as a reproductive propagule was conducted at the Wheelwright Pond Site #1, during the 1966 season and early 1967. First, 20 ungerminated winterbuds were secured to separate six foot segments of light cotton string and tethered individually to stakes scattered throughout the area in water depths ranging from 1 to 5 feet. Second, several hundred detached ungerminated winterbuds were liberated in the same areas and their progress followed daily for several weeks and weekly thereafter. Attempts to attach identifying markers restricted their free movement and were abandoned. Consequently, it was possible to observe accurately fewer than twenty-five of the total number released. Nevertheless, the results proved uniform throughout. In total, over 400 individual observations were made on a daily or weekly basis throughout the period of this study.

A 4 × 6 × 4 foot aerated aquatics tank was established in the University greenhouse for the purpose of observing the phenomenon of winterbud germination under controlled conditions particularly in response to freezing. Despite certain difficulties in controlling the growth of undesirable algae, useful data were obtained; winterbuds subjected to freezing failed to germinate.

DISCUSSION

All terminal growth, including lateral growth of the rhizome exclusive of the roots, is mediated by complex structures resembling winterbuds at all times during the year. The only obvious morphological difference between actively growing meristems and dormant winterbud structures involves size and complexity. Terminal growing points are less than 3 cm. in length and possess one lateral leaf, one shoot tip and one primordia of each meristem at any point in time. The dormant structures are essentially multiples of these, thickened transversely and containing up to ten distinct subunits arranged sequentially and/or laterally and varying in length from 3 cm. to a maximum of greater than 20 cm. Furthermore, the overwintering rhizome is tipped by a winterbud which is larger than those found during the growing season and smaller than most found at the tips of shoots in the fall. Significant anatomical and cytological differences between these unique structures are suspected based upon preliminary examinations.

Although *Brasenia* colonies are perennial, no single individual will be more than one season old; no segment of a rhizome will be more than two seasons old. Attempts to isolate the decay organisms which assist this process were inconclusive.

Winterbuds can and do germinate. However, there are limitations imposed upon such germinations by the environment. The ability of winterbuds to germinate successfully is affected by water depth. The compensation depth, beyond which germination is incomplete, lies between six and seven feet within the conditions encountered in this study. (See fig. 4) The extent to which leaf, shoot, and root development is affected by depth is pronounced, however, the physiological significance of such differences has not been investigated.

Winterbuds can not withstand freezing. In every case, the slightest degree of freezing involving meristematic tissues precluded germination.

The first winterbuds that were clearly destined to become overwintering structures were collected on July 30, 1966. The ultimate fate of such structures varied widely and is summarized in figure 5. For convenience (according to their fate within the conditions encountered by this study) it is possible to divide the production of winterbuds into two categories: (1) winterbuds maturing prior to 1 October; and (2) winterbuds maturing after 1 October. The number of winterbuds counted and observed in each category exceeds 2,500.

Winterbuds, despite the presence of an abscission-like layer at the base (Schrenk 1888, confirmed by Chrysler 1938), have not been observed to absise in the way the presence of such a structure would suggest. Abscission, other than in response to external forces, occurs naturally in response to decay of the upright stem portion near the rhizome. The largest and most complex winterbuds were collected as free-floating plant portions prior to October 1 (60% of the total production). Conversely, all winterbuds maturing after 1 October, remained attached to the parent plant unless forcibly removed (40% of the total production). With few exceptions, leaf abscission appears to function normally in both the attached and free-floating conditions. The differences between normal leaf abscission and abnormal winterbud abscission suggest the presence of a special winterbud abscission mechanism.

Fate of winterbuds associated with free-floating plant parts: All at first float. All floating winterbuds sank when their mucilage covering was reduced by approximately one half. As the temperature of the water decreased during this period, the time required for the mucilage covering to be reduced increased and the winterbuds floated longer. The sunken winterbuds either germinated and then decayed or decayed directly without visible signs of germination having occurred (fig. 2, secondary germination and fig. 3, b-c). It is probably significant that secondary (precocious) germination occurred in the fall at the same time, day-length, when germination occurred in the spring. Small groups of these partially decayed winterbuds were observed

Plate 1425

Figure 3. Winterbud structures of *Brasenia Schreberi* Gmel., illustrating the phenomena of precocious germination and decay. a. typical attached winterbud, b. precocious germination, phase 1., petiole development and elongation of apical meristems, c. precocious germination, phase 2., root development from nodal region, d. early stages of decay, e. advanced stages of decay.


e
d
c
a
b

at shoreline at the time of icing-in. Winter ice conditions would preclude their survival even were the process of decay incomplete, therefore, the natural fate of winterbuds released prior to 1 October is death.

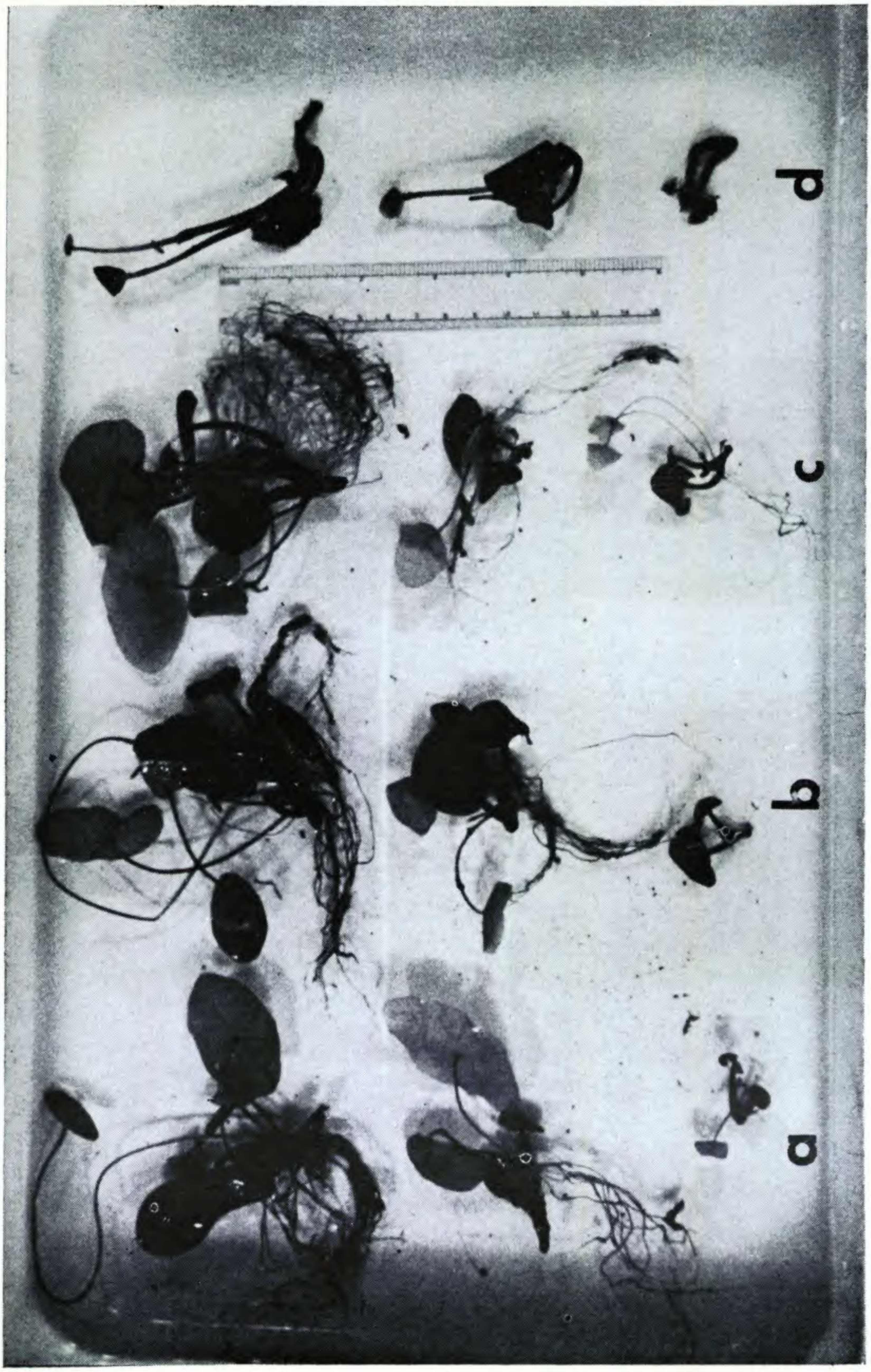
Fate of winterbuds remaining attached to parent plants after 1 October: Forty percent of the total production remained attached as of 1 October. Thirty-five percent of the total production overwintered and in the attached condition provided the source of the next year's growth. (None of the attached winterbuds were observed to germinate precociously in the fall.) Of the 5% accidentally or intentionally released, 4% of the total production were observed to float immediately and remained floating at the margins of the pond at the time of icing-in. All died. One percent, because of entanglement in other submersed vegetation were protected, at least from freezing. It is calculated that fewer than .25% of the total production possessed the potential for survival for the following reasons. (fig. 5.)

Of the many thousands of winterbuds produced in 1965 and observed to germinate in 1966, only eight produced mature plants. These were at the Nottingham site and two were collected and preserved during the summer of 1966. Of the six remaining survivors, only two survived the summer, and neither one was found again in the spring of 1967. Exactly what happened to them is not known. It is conceivable that with the spring thaw the entire plants were torn free and carried away due to their exposed position. Furthermore, the author has never observed well established *Brasenia* plants growing in swift water, not even in occasionally swift water areas.

Additional evidence supports the view that free-floating winterbuds are not effective vegetative reproductive agents.

Plate 1426

Figure 4. Results of detached winterbud germination at various depths, illustrating observable morphological differences and the compensation level below which germination was incomplete. Groups a-d, arranged according to size: < 3 cm, 3-6 cm, > 6 cm, and depth, a. 1 foot, b. 3 feet, c. 5 feet, d. 7 feet.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In the case of the tethered winterbuds (see page 424) at the Wheelwright Pond site, all germinated coterminously with the initiation of growth among the attached plants. They did so while sinking and refloating from one to several times, a factor, which if not for their tethered condition would have resulted in their floating into very shallow waters. At best, growth was limited as none of these structures were able to establish roots in the bottom muck due primarily to entanglement with established vegetation. At the end of the 1966 growing season, only one winterbud remained alive; all others had died and decayed.

Similarly, in the case of the released winterbuds, (see page 424) germination occurred as the winterbuds alternately floated and sank. Prevailing westerly winds carried most into shallow water which were then dessicated as the high waters of spring receded. The few winterbuds that survived for longer periods did so through entanglement and ultimately suffered the same fate as the tethered winterbuds.

The Nottingham beaver dam provided an unusual opportunity to witness the phenomena of winterbud germination and ultimate demise en masse. Beaver dam construction facilitates the passage of water through the structure, only in cases of very high water are beaver dams subjected to extensive overflow. Thousands of winterbuds, maturing after 1 October and surviving the winter via entanglement in existing vegetation below the ice, upon release in the spring, floated to the dam and formed an extensive mat approximately one foot thick, thirty feet wide and along the entire eighty foot length of the dam. By mid-July, the waters immediately above the dam were literally obscured by the massive growth of *Brasenia* winterbuds. By September, none remained, all had died and were decaying. The causes underlying this strange behavior have not been investigated. Among several suspected causes are, excessive crowding, competition for nutrients, lack of contact with a favorable substrate and conditions favoring decay. Several trips below the dam for a distance of two miles revealed no evidence of winterbud survival save the several plants which were previously discussed.

One additional aspect of winterbud behavior needs to be discussed concerning the presence or absence of roots at germination. Free floating winterbuds upon germination always developed roots which emerged from the nodal region from which leaves also develop. Conversely, germinating winterbuds when attached to the parent plant were never observed to form roots. In addition, winterbud-like structures found on the rhizome during the growing season (see page 425) formed roots only following the initiation of upright stems bearing leaves. Cautious speculation suggests the existence of growth substance mediation, probably in the form of an inhibition response.

A SUMMARY OF WINTER BUD ACTIVITY

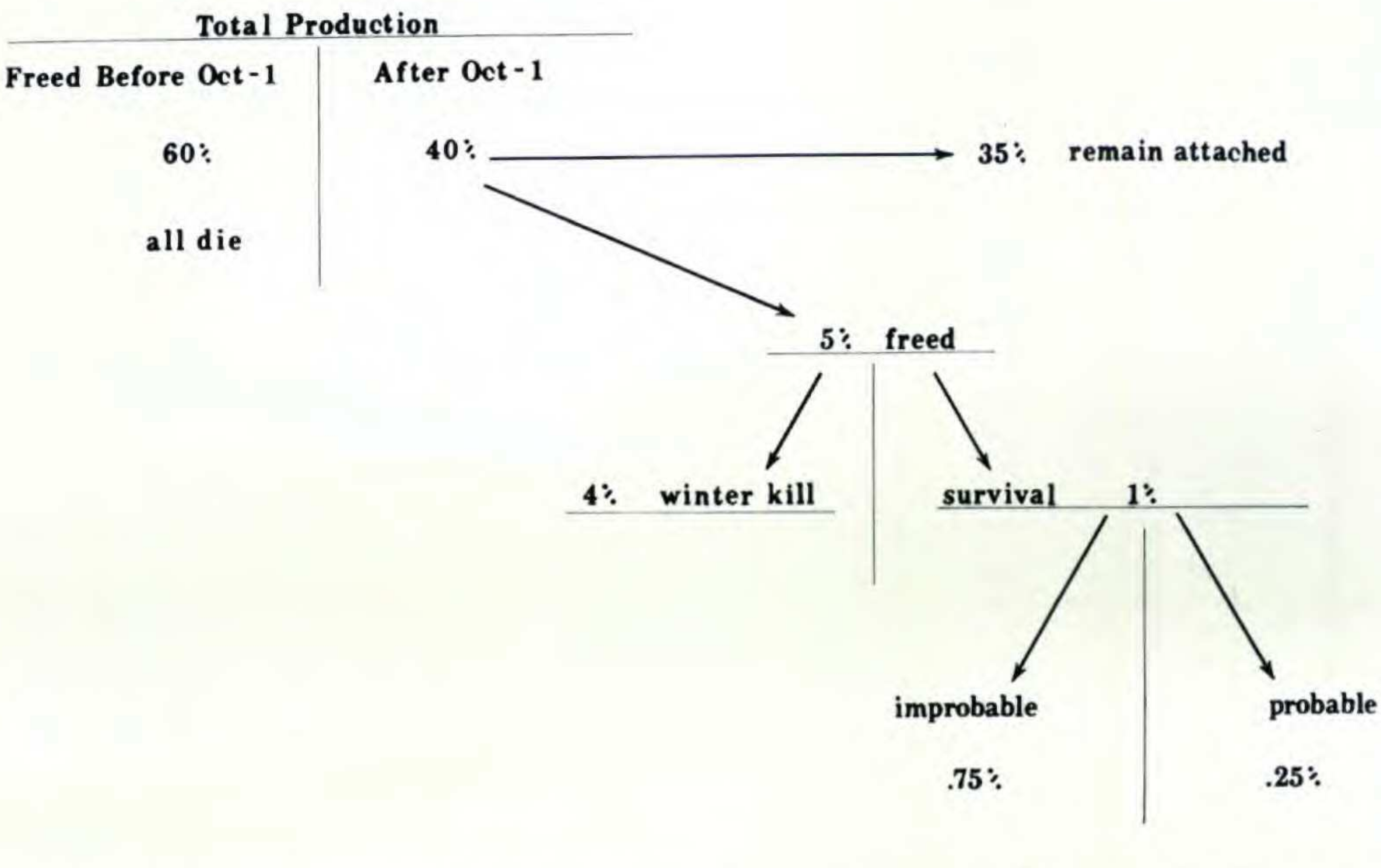

Figure 5. Summary explanation of the fate of winterbuds freed before 1 October, 1966 and those remaining attached to the parent plant or freed following 1 October, 1966. Detailed explanation in text.

SUMMARY

1. In the areas studied, the abscised winterbud structure of *Brasenia Schreberi* Gmel. is, in fact, an ineffective agent of vegetative reproduction.

2. In the areas studied, the attached overwintering winterbud structure is, in fact, absolutely essential for the annual survival of the species.

3. In the areas studied, winterbuds do not:

a. sink immediately upon abscission.

b. overwinter intact on the bottom of the pond.

c. germinate and survive, except rarely when freed.

4. If it can be demonstrated at a future time, in another climate that the winterbud does, in fact, constitute an effective agent for vegetative reproduction, it would be reasonable to conclude that the *Brasenia* winterbud has a positive survival value. Otherwise, the *Brasenia* winterbud must remain an evolutionary enigma — at best an example of Gailbraithian economics, an economy of waste.

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CYPERUS FUSCUS IN NEBRASKA AND SOUTH DAKOTA: Scattered specimens of *Cyperus fuscus* L. were found growing near colonies of *Bidens cernua* L. and *B. comosa* (Gray) Wieg. on the wet open sandy flats of the South Platte River 0.8 mile south of Sutherland, Lincoln County, Nebraska on 24 September 1968 (*Weedon* 4733, KANU). *Cyperus fuscus* L. was also found on the wet sandy clay soil along the bank of the Keya Paha River 17 miles south of Colome, Tripp County, South Dakota on 16 September 1968 (*Stephens* 29293, KANU). *Cyperus fuscus* L. is widespread in Eurasia, especially in rice fields, but appears to be rarely found in the United States. This Umbrella-sedge (galingale) has previously been reported at scattered stations from Massachusetts to western New York and Virginia. Our collections represent extensions westward from the previously known range of the species in the eastern states to areas in the Midwest. Duplicate specimens were verified as to their identification by Dr. R. L. McGregor (KANU) and by Dr. Tetsuo Koyama (NY).

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